

# Culm form analysis for bamboo, *Phyllostachys pubescens*

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**Abstract:** We investigated the culm form for one of the largest bamboo species, *Phyllostachys pubescens* Mazel ex Houz. in relation to the mechanical constraint principles, i.e., elastic, stress and geometric similarity. The fine-resolution analysis of the culm taper indicated that the culm for *P. pubescens* consisted of three or four segments with various forms, except for the butt swell. This implied that the taper of the whole culm for *P. pubescens* could be expressed by neither of these principles. The regression slope between culm height and diameter at breast height on the double logarithmic coordinates was 0.629, which was significantly different from the values predicted from these principles. In conclusion, none of these mechanical constraint principles can express the culm taper and height-diameter relationship, and there may be a need for a more complicated model to express the culm form for *P. pubescens*.

**Keywords:** culm taper; fine-resolution analysis; height-diameter relationship; mechanical constraint principle; *Phyllostachys pubescens*

## Introduction

For tree species, mechanical constraint determines its stem taper, and the three principles have been proposed to describe the mechanical design of trees as follows:

$$D(z) \propto z^{\alpha} \quad (1)$$

where  $D(z)$  is the stem diameter at a distance from the apex of the stem,  $z$ . The power exponent,  $\alpha$ , varies with the mechanical constraint principles that determine the stem taper:  $\alpha = 3/2$  when

the elastic similarity (ES: McMahon 1973; McMahon and Kronauer 1976);  $\alpha = 2$  when the stress similarity (SS: McMahon and Kronauer 1976; Dean and Long 1986);  $\alpha = 1$  when the geometric similarity (GS: King and Loucks 1978; King 1981, 1990, 1996). These mechanical principles have been applied to the height-diameter relationship as well as the stem taper (e.g., McMahon 1973; McMahon and Kronauer 1976; King and Loucks 1978; King 1981, 1990, 1996; Yamamoto 1985; Dean and Long 1986; Rich et al. 1986; Kohyama and Hotta 1990; Osawa 1992; Niklas 1995; Fransworth and Niklas 1995; O'Brien et al. 1995; Zheng et al. 1997; Inoue 2000; Matsumura 2003).

Can the culm form of a bamboo be expressed by these mechanical principles? Watanabe and Oohata (1980) studied the culm taper of a bamboo based on the pipe model theory (Shinozaki et al. 1964a, b). The culm taper of the bamboo was also analyzed for deriving a two-way volume equation (Inoue et al. 2011, 2012b; Suga et al. 2011). In addition, many studies have examined the height-diameter relationship for a bamboo (e.g., Watanabe and Oohata 1980; Watanabe et al. 1989; Inoue et al. 2012a). However, these studies aimed to predict the total culm height from the diameter at breast height. To our knowledge, there have been no studies on the culm form of a bamboo in relation to the mechanical constraint principles. Despite the different characteristics of the morphology and growth pattern compared to trees, little is known about the mechanical design of bamboo. Analysis of the culm form is not only interesting from the viewpoint of plant architecture, but it also is practically meaningful for estimating the culm volume (e.g., Inoue et al. 2011, 2012b; Suga et al. 2011).

The objective of the present study was thus to investigate the culm form for one of the largest bamboo species, *Phyllostachys pubescens* Mazel ex Houz., in relation to the mechanical constraint principles. In this study, the culm taper is defined as the change in external culm diameter along a whole culm, whereas the culm form is referred to the generic term for culm taper and height-diameter relationship. First, the culm taper for *P. pubescens* was analyzed in detail using a fine-resolution analysis (Osawa 1992). Secondly, the intraspecific relationship between total culm height and diameter at breast height for *P. pubescens* was examined. We wanted to ascertain whether the culm form for *P. pubescens* can be expressed by the mechanical constraint

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principle, i.e., ES, SS or GS principle; the detailed mechanism of mechanical design for *P. pubescens* is beyond the scope of this study.

## Materials and methods

### Site description

The data used here were collected from a stand of *P. pubescens* in a typical suburban forest, Mt. Toshima, located in the eastern part of Kumamoto City, Kumamoto Prefecture, western Japan (Inoue and Suga 2009; Inoue et al. 2011, 2012a, b; Suga et al. 2011). The average annual temperature and annual rainfall in Kumamoto City were 16.8°C and 2,060 mm, respectively (Inoue et al. 2008). Bamboo species such as *P. pubescens* were distributed from foot to mountainside of Mt. Toshima, and the upper part of this mountain was dominated by the evergreen broad-leaved trees such as *Quercus glauca* Thunb. ex Murray, *Castanopsis cuspidate* Schottky and *Symplocos lucida* Sieb. et Zucc. (Hayashi and Yamada 2008). The study site was located on a south-facing gentle slope and the altitude ranged from 80 to 90 m. According to the local residents, this site was originally used for upland farming until a few decades ago, and is now being turned into a stand of *P. pubescens* because of the planting of bamboo and subsequent abandonment.

### Field measurements

To examine the culm taper for *P. pubescens* in detail, nine healthy, living current year culms with different sizes were felled at ground level during November and December 2009 (Culm 1–9; hereafter referred to C1–C9). The culm height was measured directly with a tape measure to the nearest tenth of a meter. As Osawa (1992) suggested, the conventional methods of measuring culm diameters at only about a dozen points along the culm (e.g., Inoue and Suga 2009; Inoue et al. 2011, 2012b; Suga et al. 2011) may be insufficient to describe culm taper accurately. For this reason, the external culm diameters were recorded at numerous locations along the culm with 1-cm intervals between the apex and 50 cm from the apex; 2-cm intervals between 50 and 100 cm; 5-cm intervals between 100 and 500 cm; 10-cm intervals between 500 and 1000 cm; and 20-cm intervals through the rest of culm. The diameters at each location were measured for two orthogonal directions using a digital caliper to the nearest tenth of a millimeter, and then averaged. When a measurement point was located on the nodal part, its location was noted, since the external culm diameter on the nodal part was unusually large (Liese 1998). A list of the sample culms for the fine-resolution analysis is shown in Table 1.

To investigate the relationship between total culm height and diameter at breast height, 300 healthy, living sample culms of *P. pubescens* with various sizes were also felled at ground level from October 2008 till January 2009 and from December 2009 till February 2010. The culm height was measured directly with a tape measure to the nearest tenth of a meter. The external culm

diameter at 1.2 m height above ground level (dbh) was measured with a diameter tape or a caliper to the nearest tenth of a centimeter. A general description of sample culms for analyzing height-diameter relationship is given in Table 2.

**Table 1. List of the sample culms for the fine-resolution analysis**

Culm	Total culm height (m)	Diameter at breast height (cm)
1	5.5	2.5
2	7.6	3.2
3	9.4	4.6
4	9.1	5.1
5	11.6	6.2
6	12.4	7.5
7	15.7	8.8
8	16.7	9.9
9	17.9	11.6

**Table 2. General description of sample culms for analyzing height-diameter relationship ( $n = 300$ )**

	Total culm height (m)	Diameter at breast height (cm)
Average	13.0	8.1
Standard derivation	3.0	3.0
Maximum	19.7	14.6
Minimum	4.9	1.9
Median	8.9	8.9

### Analysis methods

For the fine-resolution analysis of the culm taper, the relationship between distance from the apex and culm diameter were plotted on the double logarithmic coordinates. Culm taper from base to apex was visually distinguished by several segments. That is to say, these segments were distinguished by interactively changing the boundaries between the segments and by comparing Eq. 1 fitted to each segment by nonlinear least squares (NLS) regression with the observed culm taper. The slope of Eq. 1 for each distinguished segment,  $\alpha$ , was determined with reduced major axis (RMA) regression technique after log-transformation (Niklas 1994). The points on the nodal parts and the butt swell were excluded from the regression analyses. The relative length for each segment relativized by the total culm height was computed.

For the analysis of the intraspecific height-diameter relationship, Eq. 2 was fitted to the relationship between total culm height,  $h$ , and dbh,  $d$ , using RMA regression after log-transformation:

$$h \propto d^{\beta} \quad (2)$$

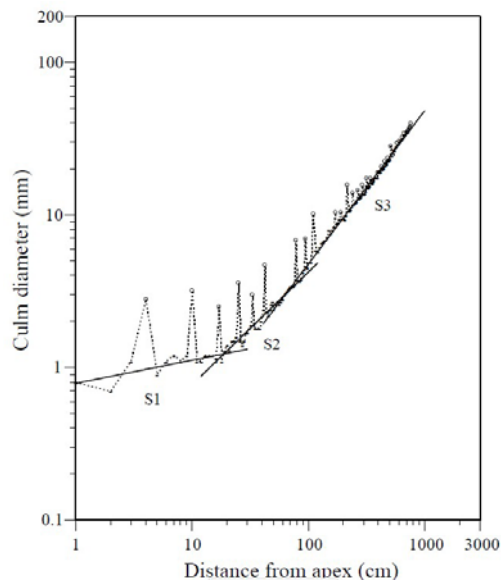
where  $\beta$  is the regression slope. The standard error of  $\beta$  with ordinary least squares regression was equal to that with RMA regression (Zhang et al. 2005). The student's  $t$ -test was used to test whether the slope  $\beta$  was different from the values predicted from three mechanical constraint principles, i.e.,  $\beta = 2/3$  (ES),  $1/2$  (SS) and unity (GS) (Niklas 1994).

## Results

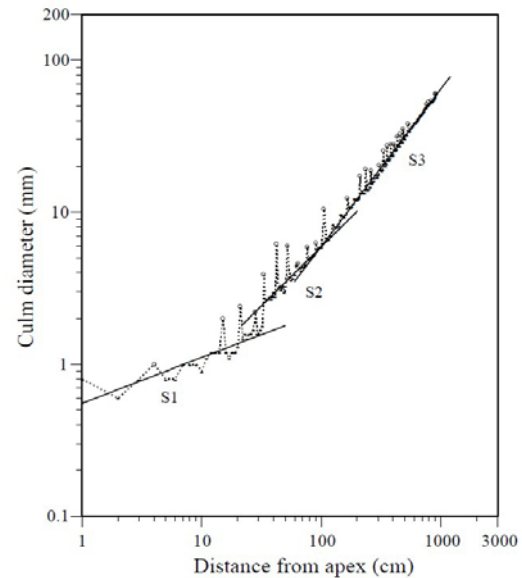
### Culm taper

The relationships between distance from the apex and culm diameter for the four *P. pubescens* sample culms are shown in Figs. 1–4. The nodal parts and butt swell are represented by open circles. The regression slope by RMA regression and relative length

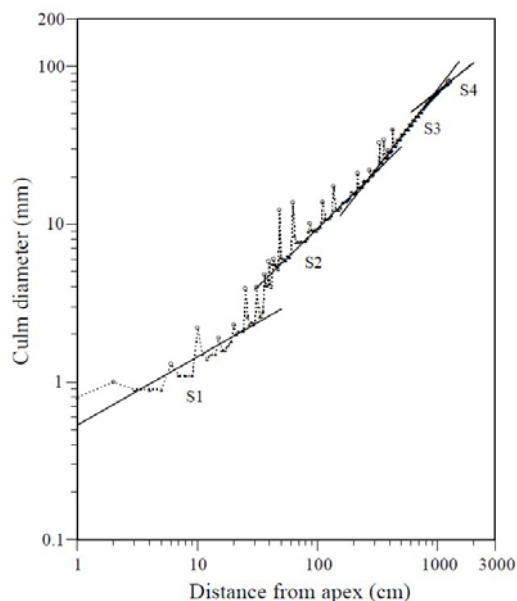
for each segment are summarized in Table 3. For all samples, the culm could be represented by three or four segments of distinctly different forms, except for the butt swell. All sample culms had the segment of which slope was approximately unity on the double logarithmic coordinates, with the values ranging between 0.982 and 1.076. Therefore, the same label, S3, is assigned to this segment of all samples, so that the distinguished segments are labeled as S1, S2, S3 and S4 downward from the apex.



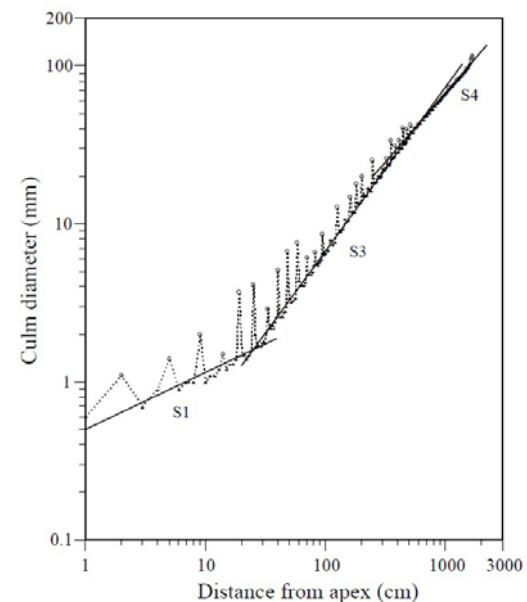
**Fig. 1** Relationships between distance from the apex and culm diameter for segments (S1, S2 and S3) of sample Culm 2. The open circles represent the points located on the nodal part and butt swell. Solid lines were fitted to each segment with NLS regression.



**Fig. 2** Relationships between distance from the apex and culm diameter for segments (S1, S2 and S3) of sample Culm 4. Legends are the same as Fig. 1.



**Fig. 3** Relationships between distance from the apex and culm diameter for segments (S1, S2, S3 and S4) of sample Culm 6. Legends are the same as Fig. 1.



**Fig. 4** Relationships between distance from the apex and culm diameter for segments (S1, S3 and S4) of sample Culm 8. Legends are the same as Fig. 1.

**Table 3. Slope and relative length for each segment determined with RMA regression**

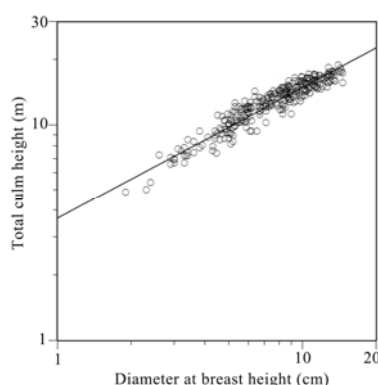
Culm	Segment 1	Segment 2	Segment 3	Segment 4
1	0.389 (6.545)	0.896 (16.182)	1.076 (77.273)	
2	0.183 (2.368)	0.773 (7.500)	1.015 (90.132)	
3	0.232 (1.596)	0.686 (6.915)	0.982 (91.489)	
4	0.333 (3.516)	0.793 (7.473)	1.037 (89.011)	
5	0.253 (2.078)	0.859 (2.771)	1.011 (67.879)	0.844 (27.273)
6	0.433 (2.823)	0.809 (22.823)	1.001 (39.677)	0.740 (34.677)
7	0.221 (1.210)	0.659 (4.013)	1.001 (58.599)	0.891 (36.178)
8	0.381 (1.976)		1.042 (51.856)	0.877 (46.168)
9	0.425 (1.117)		0.997 (49.665)	0.825 (49.218)

\* Values in the parentheses represented the relative culm length for each segment relativized by the total culm height (unit: %).

The upper segment (S1) showed the smallest and more variable slope, whose values ranged from 0.183 to 0.433. The relative length of this segment was less than 7% and was comparatively shorter than those of other segments. Although the second segment, S2, was found in C1–C7, it disappeared for the larger culms (C8 and C9). The relative length of S3 was longer than those of other segments, and the length for the smaller culms (C1–C5) reached about 70–90%. Even for the larger culms (C6–C9), the relative length of S3 ranged from 40% to 60%. The lower segment (S4) was absent for the smaller culms (C1–C4), whereas this segment occurred obviously for the larger ones (C5–C9). The slope of S4 ranged from 0.740 to 0.891, and the relative length tended to become longer as culm sizes increased.

#### Height-diameter relationship

Fig. 5 depicts the intraspecific relationship between total culm height and diameter at breast height (dbh) for *P. pubescens*. The solid line represents the regression line with RMA regression. The slope coefficient  $\beta$  by RMA regression was 0.629 (95% confidence interval 0.605, 0.652), which was significantly different from the exponents predicted from three mechanical constraint principles ( $p < 0.05$  for all principles).



**Fig. 5 Relationship between total culm height and diameter at breast height for *P. pubescens*. Solid line was fitted with RMA regression.**

## Discussion

### Culm taper

As shown in Figs. 1–4, the culm for *P. pubescens* consisted of three or four segments with different regression slopes, except for the butt swell. The culm for *P. pubescens* should be seen as an aggregation of several segments with various shapes. This shows that none of the mechanical constraint principles, i.e., ES, SS and GS principles, could express the taper of the whole culm. In other words, our data of the culm taper from *P. pubescens* would support neither of these principles. To express the taper of the whole culm for *P. pubescens* accurately, there may be a need for a more complicated model. For tree species, Osawa (1992) also concluded that a simple stem taper model with a fixed power relationship throughout the length of a tree, eq. 1, is too simplistic and does not express the observed tapers of stems successfully. This failure to express the actual tapering form with the mechanical constraint principles will be common to *P. pubescens* and tree species. The fine-resolution analysis, however, suggests several characteristics of the culm tapers for *P. pubescens* as follows:

First, a particular segment showed a comparatively similar value of the regression slope,  $\alpha$ , independent of culm sizes. It is notable that S3 has a slope of approximately unity (range 0.982–1.076). In addition, the relative length of S3 is longer than those of other segments. As shown in Table 3, the relative length reaches about 70–90% for smaller culms (C1–C5), indicating that the smaller culm for *P. pubescens* would be near a conical shape for most lengths, which is predicted by the GS principle. For *Robinia pseudoacacia* trees, Niklas (1995) also found that the stem taper for young trees complies with the GS principle. It is however obvious that the taper of S1 for the smaller culms is inconsistent with what would be expected by the GS principle. This illustrates that the whole culm for the smaller *P. pubescens* strictly shows a different shape from that expected from the GS principle. Moreover, the regression slopes of other segments (S1, S2 and S4) for the larger culms (C6–C9) are gentler than the values predicted by the three principles, and the relative length for S3 also decreases to 40–60% as culm sizes get larger. Hence, none of these principles appear appropriate to describe the taper throughout the length of the larger culms as well as the smaller ones.

Secondly, a size-dependent pattern of culm taper is found. As culm sizes increased, S2 disappeared and S4 appeared. The length of S4 then becomes longer gradually and could reach the same length as S3. Such pattern may be apparent when the culm sizes are about the sizes of C5–C8.

### Height-diameter relationship

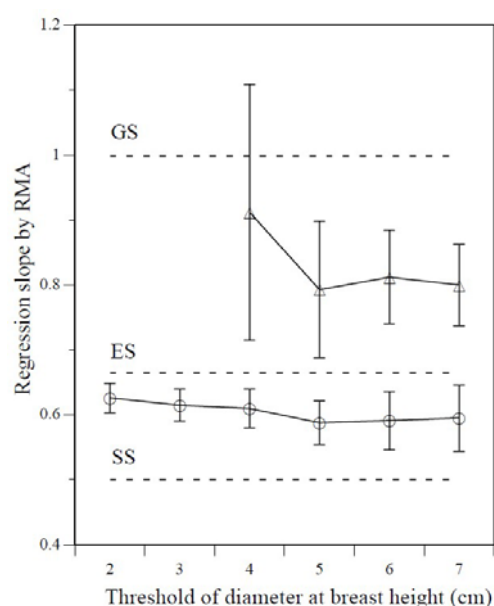
Osawa (1992) reported that the height-diameter relationship for *Abies sachalinensis* var. *sachalinensis* may be consistent with what is expected from the ES principle (the regression slope was

0.694; 95% CI 0.638, 0.755). Whittaker and Woodwell (1968) found the regression slope by RMA regression was 0.70 for *Quercus coccinea*, indicating that the height-diameter relationship for *Q. coccinea* is compatible with the ES principle. For the adult canopy trees of tropical forests, the regression slope equals to or is greater than that predicted by the ES principle (e.g., Fransworth and Niklas 1995; O'Brien et al. 1995; King 1996), whereas the saplings of canopy and understory trees conform to the GS principle (e.g., King 1990; Kohyama and Hotta 1990). In addition, the ES principle is well fitted to the relationship between tree height and dbh for various species such as *Cryptomeria japonica* D. Don (Yamamoto 1985; Inoue 2000; Matsumura 2003), *Chamaecyparis obtusa* Endl. (Yamamoto 1985), *Neobalanocarpus heimii* (Matsumura 2003), *Pinus sylvestris* var. *mongolica* and *Larix principis rupprechtii* (Zheng et al. 1997). These facts indicate that the ES principle will work well for expressing the relationship between height and dbh for tree species, except for the sapling trees. One of the plausible mechanisms of the height-diameter relationship for tree species is as follows: when in sapling stage, the height-diameter relationship for canopy trees conforms to the GS principle, since the sapling trees vest more resources in rapid height growth to achieve a certain height (King 1981). As trees grow larger, the relationship is then consistent with the ES principle, since stability may be favored over rapid height growth in adult trees (King 1996). For these reasons, the ES principle may be violated to express the height-diameter relationship for tree species, including small and intermediate-sized trees (e.g., O'Brien et al. 1995; Niklas and Spatz 2004).

The result of the present study indicated that the regression slope  $\beta$  of the height-diameter relationship for *P. pubescens* by RMA regression was significantly different from the value predicted by the mechanical constraint principles. As mentioned above, the height-diameter relationship for tree species would follow the different principles dependent on their stem sizes. Do the different principles also govern the height-diameter relationships for larger and smaller *P. pubescens*? To examine the dependency of the mechanical constraint principles on the culm sizes, all sample culms were bisected into larger and smaller culms by a given threshold of dbh, and then the regression slopes  $\beta$  for the larger and smaller culms were determined with RMA regression. Changes in the regression slopes with the thresholds of dbh are given in Fig. 6. When the threshold was 2 cm, the number of smaller culms was one, and hence the regression slope for the smaller culm could not be determined. When the threshold was 3 cm, the regression slope for the smaller culms showed a comparatively larger variation (95% CI 0.285, 1.951) and was different from the values expected by none of the three principles. Hence, the regression slopes for the smaller culms divided by 2 and 3 cm in thresholds of dbh are not shown in this figure.

The regression slope was significantly different between the larger and smaller culms ( $p < 0.05$  for all thresholds), suggesting that the height-diameter relationships for the large- and small-sized culms would conform to the different mechanical constraint principles. As with the culm taper, a simple height-diameter model given by eq. 2 may be too simplistic and does

not express the height-diameter relationship across a wide range of culm sizes. Moreover, the regression slope for the larger culms was significantly different from 2/3 ( $p < 0.05$  for all thresholds), indicating that the height-diameter relationship for the larger *P. pubescens* is inconsistent with what is expected from the ES principle. Although the regression slope for the small-sized culms divided by 4 cm in the threshold was compatible with the GS principle ( $p > 0.05$ ), the slope by other threshold was a different matter ( $p < 0.05$  for all). These facts suggest that the height-diameter relationships for both large- and small-sized culms might govern the different principles examined in this study. Therefore, the mechanical constraint principles, i.e., ES, SS and GS principles, are not acceptable for the height-diameter model for *P. pubescens*, and there may be a need for a more complicated model to express the height-diameter relationship as well as the culm taper.



**Fig. 6** Changes in regression slopes for larger and smaller culms by RMA with the threshold of diameter at breast height. The open circle and triangle indicate the regression slopes for the larger and smaller culms, respectively. The error bar shows 95% confidence interval of the regression slope. The broken lines represent the regression slopes expected by SS, ES and GS mechanical constraint principles.

## Conclusions

In the present study, the culm form for *P. pubescens* was analyzed in relation to the mechanical constraint principles, i.e., ES, SS and GS principles. Fine-resolution analysis of the culm taper reveals that the culms consist of three or four segments with different forms except for the butt swell. The regression slope between culm height and dbh on the double logarithmic coordinates is significantly different from the values predicted by these principles. In conclusion, none of these mechanical principles can express the culm taper and height-diameter relationship, and

there may be a need for a more complicated model to express the culm form for *P. pubescens*.

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